

The contribution of coarse woody debris to carbon, nitrogen, and phosphorus cycles in three Rocky Mountain coniferous forests

Raija Laiho and Cindy E. Prescott

Abstract: The contribution of coarse woody debris to C, N, and P cycles was assessed in forests of lodgepole pine (*Pinus contorta* Dougl. ex Loud.), white spruce (*Picea glauca* (Moench Voss), and subalpine fir (*Abies lasiocarpa* (Hook.) Nutt.) – Engelmann spruce (*Picea engelmannii* Parry ex Engelm.) in southwestern Alberta. Mass loss and changes in C, N, and P concentrations in decomposing log segments were measured for 14 years. Litter input was measured during 10 years for coarse woody debris, 1 year for ground vegetation, and 5 years for other aboveground litter types. Release of C, N and P from decomposing litter were simulated for a period of 40 years. After 14 years, log segments of pine, spruce, and fir had lost on average 71, 38, and 40%, respectively, of their dry mass. The N content of the pine logs increased, spruce changed little, and fir lost N. Phosphorus accumulated in all logs. The greatest imports of N and P occurred at the pine sites and fir sites, respectively, where these nutrients were the least available, indicating that wood decay organisms may compete with vegetation for limiting nutrients in these forests. Coarse woody debris comprised 3–24% of aboveground litter and contributed less than 5% of the N and P released. Coarse woody debris does not appear to make a significant contribution to N and P cycling in these forests.

Résumé : La contribution des débris ligneux grossiers aux cycles de C, N et P a été évaluée dans des forêts de pin lodgepole (*Pinus contorta* Dougl. ex Loud.), d'épinette blanche (*Picea glauca* (Moench) Voss) et de sapin subalpin (*Abies lasiocarpa* (Hook.) Nutt.) – épinette d'Engelmann (*Picea engelmannii* Parry ex Engelm.) dans le sud-ouest de l'Alberta. La perte de masse et les changements dans les concentrations de C, N et P dans des segments de billes au sol en décomposition ont été mesurés pendant 14 ans. L'apport de litière a été mesuré pendant 10 ans dans le cas des débris ligneux grossiers, 1 an dans le cas de la végétation au sol et 5 ans dans le cas des autres types de litière épigée. La libération de C, N et P dans la litière en décomposition a été simulée pour une période de 40 ans. Après 14 ans, les segments de billes au sol de pin, d'épinette et de sapin avaient perdu en moyenne respectivement 71, 38 et 40% de leur masse sèche. Le contenu en N des billes de pin a augmenté, il a peu changé chez l'épinette et a diminué chez le sapin. Le contenu en phosphore a augmenté dans toutes les billes. Les plus fortes importations de N et de P sont survenues respectivement dans les sites avec pin et dans les sites avec sapin, là où ces nutriments étaient les moins disponibles, ce qui indique que les organismes responsables de la décomposition du bois sont probablement en compétition avec la végétation pour les nutriments qui sont déficients dans ces forêts. Les débris ligneux grossiers représentaient 3 à 24% de la litière épigée et contribuaient moins de 5% de N et de P rendus disponibles. Les débris ligneux grossiers ne semblent pas apporter une contribution significative au cyclage de N et P dans ces forêts.

[Traduit par la Rédaction]

Introduction

With the current trend towards more natural management of forests, the role of coarse woody debris (CWD) in forest ecosystems has received increasing attention. An obvious difference between natural and managed forests is the relative scarceness of CWD in managed forests (e.g., Andersson and Hytteborn 1991). The role of CWD as a critical habitat element for many species of animals, plants, and fungi is well recognized (Freedman et al. 1996). Less is known about

the role of CWD in element cycling and productivity of forest ecosystems (Harmon et al. 1986). Studies in the coastal forests of the Pacific Northwest, where CWD is particularly abundant and large (Harmon et al. 1986; Sollins et al. 1987; Keenan et al. 1993), have suggested that CWD is an integral component of forest ecosystems, acting as a long-term stabilizing storage pool for nutrients. In other coniferous forests, the role of CWD in nutrient cycling has been found to be small (Busse 1994). There is some controversy as to how critical CWD is to forest productivity (Fahey 1983; Harmon et al. 1986; Spies et al. 1988).

Assessing the role of CWD in element cycling requires measurements of the rates of input and decomposition of CWD relative to other litter types. The long time span and considerable temporal variation makes it difficult to directly measure CWD input and decomposition. Most previous studies have relied on indirect methods for estimating rates of decomposition and have usually involved chronosequence techniques. Decomposition estimates have usually been based

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on log inventories using various back-dating techniques (e.g., Sollins et al. 1987; Brown et al. 1998), and changes in wood density have usually been reported, as the original mass of the logs was not known (Graham and Cromack 1982; Fahey 1983; Means et al. 1985; Sollins et al. 1987; Alban and Pastor 1993). In other studies, the mass of CWD was inventoried and rates of decay were estimated with the assumption of constant input (Sollins 1982). Grier (1978) and Stone et al. (1998) reported volume losses of CWD based on a single remeasurement. Because earlier studies have measured different variables over vastly different time periods, the decay rates (k values) presented may represent quite different aspects of the decomposition process (Lambert et al. 1980; Stone et al. 1998). These rather coarse estimates may be adequate for management guidelines, but ecosystem models require more precise information on the pattern of mass loss and nutrient release from CWD.

In this study, the rate of CWD input (treefall) was measured for 10 years in three Rocky Mountain forests: a self-thinning lodgepole pine (*Pinus contorta* Dougl. ex Loud.) forest, a mature white spruce (*Picea glauca* (Moench) Voss) forest, and an old-growth forest of Engelmann spruce (*Picea engelmannii* Parry ex Engelm.) and subalpine fir (*Abies lasiocarpa* (Hook.) Nutt.). Mass loss and changes in C, N, and P concentrations were measured over a 14-year period in portions of recently fallen logs of the dominant species in each forest (pine, spruce, and fir, respectively). The role of CWD in nutrient cycling in these forests was assessed by determining (i) the proportion of the annual aboveground inputs of C, N and P that is derived from CWD and (ii) the proportion of the C, N, and P released from aboveground litter during a simulated 40-year period that is derived from CWD.

Study sites

The study sites were in the Kananaskis Valley, in the Front Range of the Rocky Mountains of southwestern Alberta (51°2'N, 115°3'W). The Kananaskis Valley has a dry continental climate with warm, dry summers and long, cold winters modified by intermittent warm (chinook) winds. Average monthly temperatures range from -10°C in January to 14°C in July. Average annual precipitation is 660 mm, of which 290 mm occurs as snow. Soils are well-drained brunisols overlying primarily limestone glacial deposits.

Forests in the Kananaskis Valley are predominantly coniferous, with a montane zone of lodgepole pine and white spruce or white × Engelmann spruce hybrids below 1700 m and an upper subalpine zone of Engelmann spruce (*Picea engelmannii* Parry ex Engelm.), or spruce hybrids, and subalpine fir. The distribution of forests in the montane zone reflects the predominance of disturbance by fire. Lodgepole pine regenerates rapidly after severe fires, often forming dense, even-aged stands. Spruce also regenerates immediately after fire on moister sites with an adequate seed source. After canopy closure, spruce and fir dominate the understorey but rarely replace the pine before the next fire. In the subalpine zone, fires are less frequent, and the forests are dominated by spruce and fir.

The three study sites were within 5 km of one another in the Lusk Creek basin, adjacent to the Kananaskis Field Station of the University of Calgary. The sites were identified according to the dominant species of overstorey tree in the stand as pine, spruce, or fir. The sites are described in more detail by Prescott et al. (1989a).

The pine site was located on a flat ground moraine of glacial till at 1530 m elevation. The soil was an Orthic Eutric Brunisol of clay loam texture overlying glacial till. Canopy trees were exclusively lodgepole pine and originated after a severe fire destroyed a similar stand in 1889. Spruce, balsam poplar (*Populus balsamifera* L.), and trembling aspen (*Populus tremuloides* Michx.) dominated the understorey. The shrub layer was composed of buffalo-berry (*Shepherdia canadensis* (L.) Nutt.), Scouler willow (*Salix scouleriana* Barr. ex Hook.), and common juniper (*Juniperus communis* L.). Ground vegetation was dominated by forbs (*Cornus canadensis* L., *Hedysarum sulphurescens* Rydb., *Lathyrus ochroleucus* Hook., *Aster conspicuus* Lindl., *Epilobium angustifolium* L.), and grasses (*Calamagrostis rubescens* Buckl., *Elymus innovatus* Beal.). Stand density in the beginning of the study period (1984) was 1716 stems/ha, stand basal area was 30.5 m²·ha⁻¹, and mean diameter at breast height (DBH) was 12.2 cm.

The spruce site was on a northwest facing 3° slope at 1500 m elevation. The soil was an Orthic Eutric Brunisol of sandy loam texture overlying lake deposits. The overstorey was composed of spruce and pine, most of which originated from a fire in 1865. The understorey was also predominantly white spruce, along with Douglas-fir, aspen, poplar, buffalo-berry, and green alder (*Alnus crispa* (Ait.) Pursh). Ground vegetation was composed of mosses (*Pleurozium schreberi* (Brid.) Mitt., *Hylocomium splendens* (Hedw.) B.S.G.), twinflower (*Linnaea borealis* L.), and forbs (*Aster conspicuus*, *Epilobium angustifolium*, *Arnica cordifolia* Hook., *Mertensias paniculata* (Ait.) G. Don). Stand density was 750 stems/ha, basal area was 39 m²·ha⁻¹, and mean DBH was 16.4 cm.

The fir site was situated at 1830 m on a 30° slope facing west-northwest. The soil was an Orthic Eutric Brunisol of clay loam texture overlying colluvial deposits. The overstorey was composed of subalpine fir up to 200 years old and Engelmann spruce up to 350 years old. Spruce and fir were both present in the understorey along with green alder and mosses (*Hylocomium splendens*, *Pleurozium schreberi*). Stand density was 1177 stems/ha, basal area was 40 m²·ha⁻¹, and mean DBH was 11.6 cm.

Methods

Wood decomposition

Standing dead or recently fallen trees approximately 15 cm in diameter were harvested and cut into segments 20 cm long with a fine blade band saw. Only logs of the dominant species at each site were harvested; the total number of logs collected from each site was three pine, three spruce, and four fir. The bark was still intact, so collection was probably within 5 years of the death of the tree. Three-centimetre pieces were cut from each end of each log segment, all pieces were weighed, and a metal tag was attached to one of the end pieces. The two end pieces were then reattached to the log with a 4-cm screw. This was done to reduce artificial exposure of heartwood in the central piece, which was to be used to determine the rate of decay. This also allowed us to estimate the effect of artificial exposure by comparing the decay rate of center and end pieces. In September 1984, seventy log segments were placed on the litter surface at 3-m intervals within one 20 × 30 m plot at each site. Only logs of the one dominant tree species at each site were placed at the site. Unused portions of the harvested logs were used to determine the average moisture content and C, N, and P concentrations; hence, the original dry mass and C, N, and P content of each log segment.

Ten log segments were collected from each site after 2, 6, 10, and 14 years. Where logs had partially disintegrated, small pieces of bark that were clearly part of the original segment were also included in the sample. Logs were cleaned of litter and vegetation, and end pieces were removed. Each piece was weighed fresh, dried

at 80°C to constant mass, and weighed. The central pieces were then ground for C, N, and P analyses.

Litter input

Input of CWD (treefall) was estimated on two 20 × 30 m plots at each site. All fallen trees were marked with paint in August 1984. New (unmarked) downed trees were checked annually for the first 5 years and once again after another 5-year period. At each time, the species and decay class of each downed tree was recorded, and their DBH and length (within the plot) were measured. Decay classes (adapted from Triska and Cromack 1979) were based on visual properties of the logs, ranging from wholly intact (decay-class 1) through loss of bark and twigs (decay-class 2), loss or branches and softening of wood (decay-class 3), and fragmentation and incorporation into the forest floor (decay-classes 4 and 5). After calculating the stem volumes using these dimensions, the total dry mass and C, N, and P content of each log was estimated using average density values and nutrient concentrations for each species – decay-class combination. These averages were estimated from one to eight samples of each species – decay-class combination collected from outside the plots as described by Prescott et al. (1989b). Trees were not considered to be litter input until they were in contact with the ground, by which time most had been standing dead for several years and were in decay-class 2.

Input of “small woody litter,” i.e., twigs (diameter < 1 cm), branches (diameter ≥ 1 cm), intact female cones, and bark, was harvested annually for 5 years on ten 3 × 3 m plots at each site. “Nonwoody litter” from trees and large shrubs, i.e., needles, leaves, male cones, female cone scales, and seeds was collected in fifteen 0.25-m² litter traps placed randomly in one 20 × 30 m plot at each site. The traps were emptied monthly or bimonthly during the first 3 years, and twice a year, in late summer and autumn during the period of highest litterfall (Prescott et al. 1989b), during the next 2 years. Litter input from ground vegetation was estimated during 1985 as described by Prescott et al. (1989b).

The litter samples were separated into components and dried to constant mass at 80°C. Carbon, N, and P concentrations were analyzed in five composite samples of each litter type, i.e., small woody litter, nonwoody litter, and ground vegetation, and used to estimate the mass of nutrients in the annual inputs of each litter type. Inputs of mass and C were examined in more finely separated litter types: foliage, fine woody debris (FWD; twigs, branches, and bark), and reproductive organs (male and female cones, cone scales, seeds), CWD, and ground vegetation.

Chemical analyses

All samples except the 14-year decomposed logs were analyzed in the Department of Biological Sciences at the University of Calgary, Calgary, Alta. Samples were ground in a Wiley mill and C concentrations were measured with a Leco carbon analyzer. Nitrogen and P concentrations were analyzed with a Technicon II autoanalyzer after a sulphuric acid – hydrogen peroxide digestion in 360°C (Lowther 1980). The 14-year decomposed logs were analyzed in the Soil Science Department at University of British Columbia, Vancouver. Carbon was measured with a Leco carbon analyzer and N and P concentrations were analyzed with a Lachat autoanalyzer following the digestion procedure of Parkinson and Allen (1975). Nutrients concentrations were measured only in the original and 14-year logs.

Statistical analyses

Three equation types were tested to describe the pattern of mass loss from logs over time: linear, exponential, and sigmoidal. Linear and exponential equations have been used in earlier studies of wood decomposition, and a sigmoidal curve was suggested by lo-

Table 1. Decomposition rate constants for various litter types in the three forests, used in the decomposition simulation (adapted from Taylor et al. 1991).

Litter type	Pine	Spruce	Fir
Ground vegetation and leaves	0.20	0.20	0.20
Pine needles	0.1151	0.1735	—
Spruce needle	—	0.1828	—
Fir needles	—	—	0.0933
Twigs	0.0549	0.0549	0.0620
Branches	0.0521	0.0265	0.0353
Bark	0.05	0.04	0.03
Female cones	0.0307	0.0691 ^a	0.0437 ^a
Other reproductive organs	0.0440	—	—

^aUsed for all reproductive organs.

cally weighted regression procedures used for preliminary smoothing of the data. Statistical outliers in the wood decomposition data were identified and excluded from the regression analyses. Nonlinear estimation was done using a Gauss–Newton method that computes exact derivatives and a least squares loss function (SYSTAT Inc. 1996). Final equation forms were selected after checking the residuals and assessing the bias of the estimates.

The relationship between moisture and decomposition was investigated with Pearson correlations between moisture content and percent mass loss of the logs after 14 years. A Mann–Whitney test was used to determine if moisture content and percent mass loss differed between moss-covered and uncovered spruce logs.

The data on differences in mass loss between end and center pieces of the log segments were strongly heteroscedastic, which could not be remedied with transformations. Consequently, nonparametric tests were used for comparing decomposition of end and center pieces. The Friedman test, corresponding to repeated measures analysis of variance with one group, was used to determine if the difference changed over time, and the Wilcoxon signed ranks test was used to test for differences in mass remaining of end and center pieces of each species and at each sampling time.

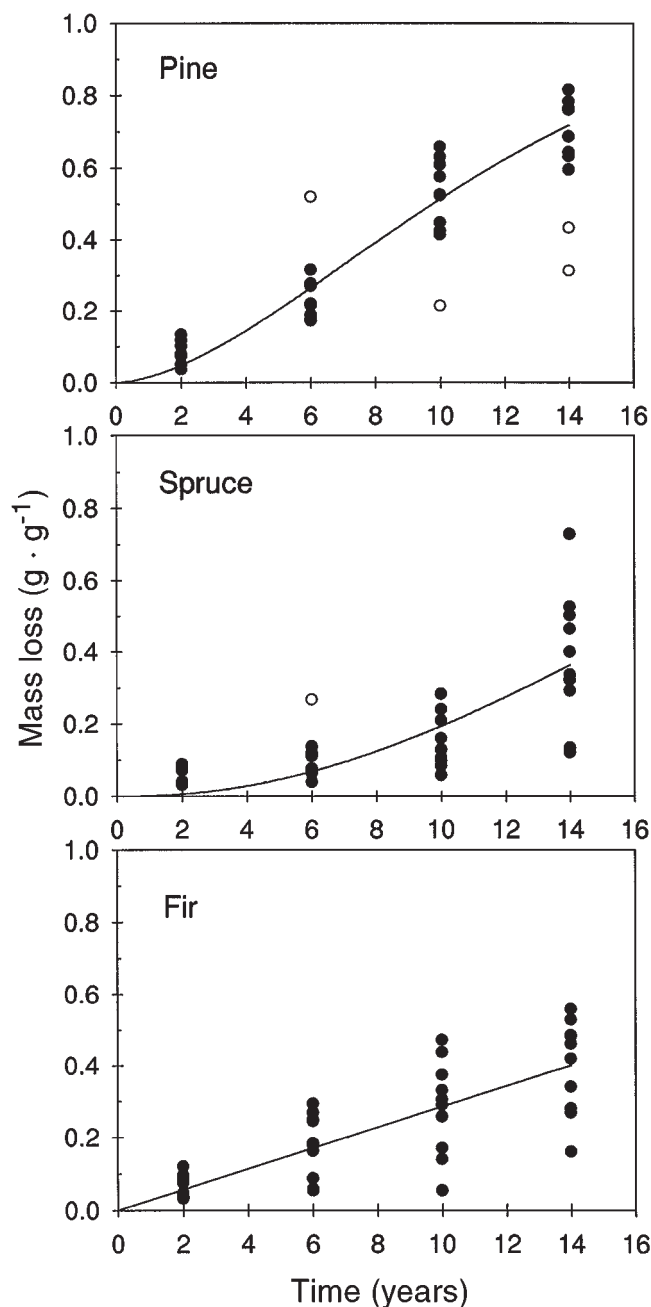
Organic matter accumulation, decomposition, and nutrient release simulations

To examine the relative importance of the litter types in the nutrient cycles of these forests, organic matter accumulation and annual release of C, N, and P from each litter type were simulated for a period of 40 years. A 1-year time step was used; each year, the mean annual litter input of each litter type was added to the system. Mass loss equations from the log decomposition experiment were used for CWD. Decomposition of other litter types was simulated using the negative exponential decay model (e.g., Olson 1963)

$$[1] \quad \text{Mass remaining at time } t / \text{initial mass} = e^{-kt}$$

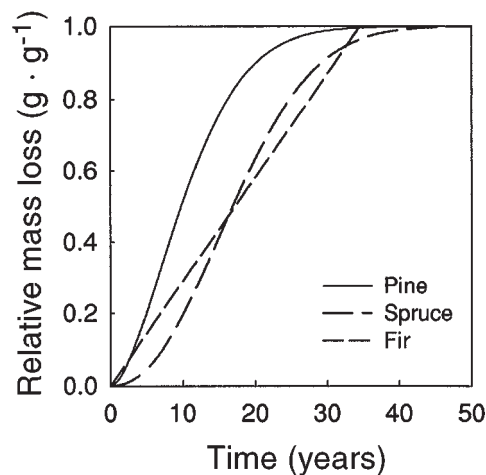
with the decomposition constants (k values) presented in Table 1. For materials for which decomposition data were not available, the k value for a material most similar to it was used (e.g., k values for *Epilobium angustifolium* were used for all herbaceous materials). Each litter cohort was progressively decomposed until the mass of the cohort became negligible or the simulation period ended. Organic matter accumulation was then calculated as the sum of the remaining mass of each cohort at each time step, and annual decomposition as the mass lost from each cohort between the time steps. Initial concentrations of C, N, and P in each litter type are in Table 2. Release of N and P was simplified by assuming nutrients

Fig. 1. Dry mass loss as proportion of original mass for log segments of lodgepole pine, white spruce, and subalpine fir at the pine, spruce, and fir sites, respectively. Equations for the regression curves are in Table 3. Open circles show outliers that were excluded from the regression analyses.



were lost at the same rate as mass. Although this may not capture the net accumulation of nutrients common in the early stages of decomposition, it should accurately estimate the release of the nutrients originally in the litter over the entire decomposition period. Increases in nutrient concentrations observed in decomposing litter may result from external inputs such as import from the surroundings by fungal hyphae (Wells and Boddy 1990), and nitrogen fixation in decaying wood (Jurgensen et al. 1987). This is an important aspect of the role of litter in nutrient cycling, but here we address only the contribution of the nutrients originally in the litter.

Fig. 2. Projected mass loss for log segments of lodgepole pine, white spruce, and subalpine fir at the pine, spruce, and fir sites, respectively, based on regression equations in Table 3.



Results

Wood decomposition experiment

After 14 years, most logs at the spruce site were overgrown by mosses (*Hylocomium splendens*, *Pleurozium schreberi*, *Ptilium crista-castrensis*). The bark beneath the log had disintegrated and was impossible to separate from the litter and root material beneath the log. The proportion of bark remaining in the upper part varied among logs. The wood was not fragmented when undisturbed but broke into pieces when handled. Fine roots were abundant in the bark and between the bark and wood, and there was some growth into the wood. The pine logs had less litter or moss (*Brachytecium* sp.) cover; however, the lower third of most logs was buried in the forest floor, and most of the bark was gone. The wood was soft and fragmented easily when handled. There were abundant fine roots in the wood. The fir logs were solid, and most still had their bark, which was tightly attached to the wood. They had very little if any litter or moss cover but were partly buried in the forest floor.

Pine logs (center pieces) lost on average $71 \pm 8\%$ (mean \pm SD) of their mass during the 14-year study period (Fig. 1). For spruce and fir the corresponding values were $38 \pm 18\%$ and $40 \pm 13\%$, respectively. For pine, in which decomposition had proceeded furthest, mass loss could be best predicted with a sigmoidal function (Fig. 1, Table 3)

$$[2] \quad \text{Mass loss} = 1 - e^{-(\text{time} \times P_1)^{P_2}}$$

A similar equation was fitted to the data for the spruce logs. In fir logs, however, the mass loss during the study period was best described by a linear function. By extending the curves fitted to each of the log types, we could estimate the number of years required for logs of each species to disappear. Assuming that these patterns of mass loss continue, the pine and fir logs would disappear in ca. 35 years, and spruce logs in 45 years (Fig. 2)

Percent mass loss was positively correlated with moisture content at time of harvest in spruce and fir logs ($p = 0.014$ for spruce and 0.040 for fir) but not in pine logs ($p = 0.380$).

Table 2. Carbon, nitrogen, and phosphorus concentrations of the different litter types used in the simulation.

	% C	mg N·g ⁻¹	mg P·g ⁻¹
Pine site			
CWD	47.76±0.44	0.61±0.12	0.04±0.02
Small woody litter	50.98±0.41	2.55±0.27	0.23±0.03
Nonwoody litter	51.27±0.29	5.77±0.21	0.50±0.03
Ground vegetation	46.82±0.89	11.45±1.14	1.89±0.22
Spruce site			
CWD	49.07±0.82	0.88±0.20	0.03±0.00
Small woody litter	51.67±0.14	5.45±0.23	0.47±0.05
Nonwoody litter	49.14±0.36	5.76±0.25	0.84±0.08
Ground vegetation	44.15±0.62	12.24±2.47	2.58±0.51
Fir site			
CWD	49.76±0.59	1.55±0.35	0.01±0.01
Small woody litter	52.82±0.43	6.62±0.56	0.54±0.09
Nonwoody litter	50.57±0.58	8.20±0.71	0.55±0.06
Ground vegetation	43.68±0.40	14.35±2.15	1.07±0.15

Note: Coarse woody debris (CWD) concentrations are the initial concentrations of the log decomposition experiment material, for other types, concentrations are from Prescott et al. (1989b). Values are mean ± SD.

Table 3. Mass loss equations for pine, spruce, and fir logs based on the data from the 14-year log decomposition field experiment.

	P_1	SE	P_2	SE	R^2	SEE
Mass loss = $1 - e^{-(\text{time} \times P_1)^{P_2}}$						
Pine	0.082	0.002	1.67	0.13	0.968	0.068
Spruce	0.050	0.006	2.20	0.48	0.802	0.106
Mass loss = $P_1 \times \text{time}$						
Fir	0.029	0.002			0.877	0.100

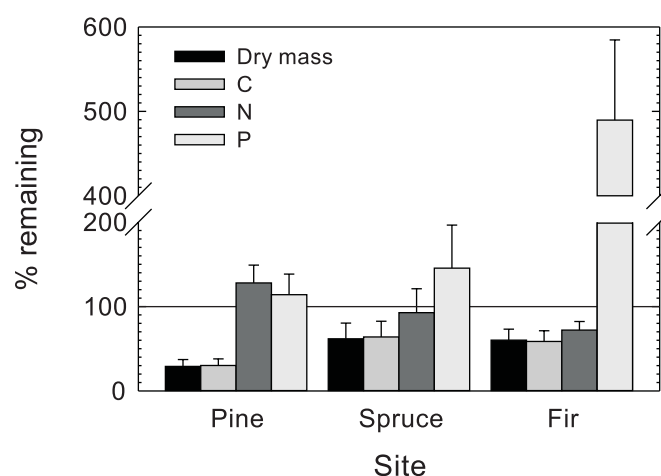
Spruce logs that were completely overgrown by mosses by 14 years had a higher ($p = 0.028$) moisture content than logs with little or no cover. They had also lost on average slightly more of their original mass, although the difference was not statistically significant ($p = 0.465$).

After 14 years, end pieces were still tightly connected to the center piece, and often some force was required to separate them as fungal growth “sealed” the pieces. End pieces decomposed faster than center pieces over the 14-year decomposition period, and this difference increased with time ($p = 0.018$ for pine, 0.007 for spruce, and 0.002 for fir). Average mass loss in the end pieces was $4 \pm 7\%$ greater than in the center pieces of pine logs, $4 \pm 8\%$ greater in spruce, and $10 \pm 7\%$ greater in fir after 14 years. Mass loss from ends and centers were not significantly different in pine logs at any sampling time. In spruce logs, mass loss from end pieces was significantly greater than from center pieces after 10 years. In fir logs, mass loss from end pieces was significantly greater than from center pieces at all sampling times except 2 years. There was actually less mass lost from the end pieces of both spruce and fir logs during the first 2 years.

Carbon concentrations in the decaying log segments changed little during the 14 years, whereas N and P concen-

Table 4. Carbon, nitrogen, and phosphorus concentrations of the log segments after 14 years of decomposition.

Site	% C	mg N·g ⁻¹	mg P·g ⁻¹
Pine	49.77±1.65	2.78±1.08	0.16±0.06
Spruce	50.84±1.08	1.53±0.92	0.08±0.04
Fir	48.44±0.91	2.03±0.94	0.09±0.05

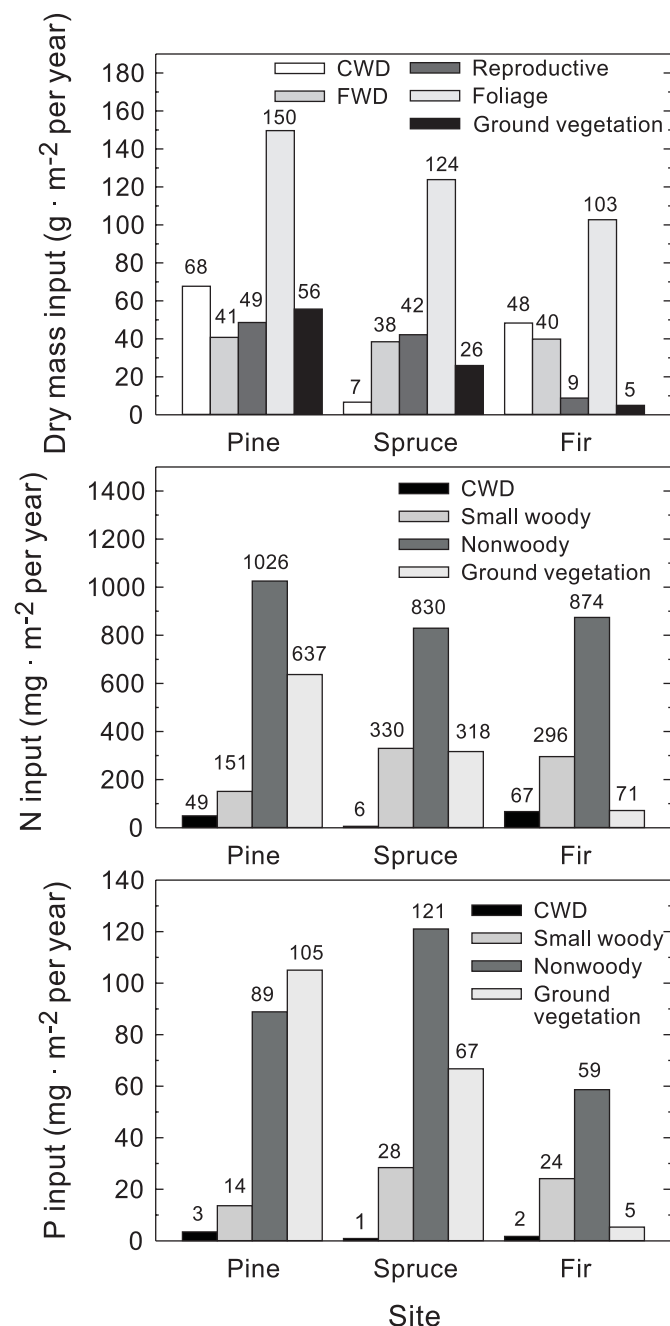
Fig. 3. Dry mass, C, N, and P contents of 20-cm log segments of lodgepole pine, white spruce, and subalpine fir after decomposing for 14 years at the pine, spruce, and fir sites, respectively. Values are relative to the initial content; values above 100% indicate net import, values below 100% indicate net release. Each value is the mean of 10 log segments Error bars are 1SD.

trations increased (Table 4; initial concentrations in Table 2). The percentage of the original C content remaining after 14 years was similar to the percentage of the original mass remaining (Fig. 3). Over the 14-year decomposition period, the N content of pine logs increased, spruce logs changed little, and fir logs lost almost 30% of their initial N. This corresponded to an average net import of 0.78 ± 0.65 mg N·g⁻¹ remaining mass in each pine log, a net release of 0.05 ± 0.40 mg N·g⁻¹ from spruce logs, and net release of 0.65 ± 0.55 mg N·g⁻¹ from fir logs. Phosphorus accumulated in decaying wood of all three species, particularly in fir logs which had final P contents nearly five times greater than their initial contents (Fig. 3). The amounts of P that had been imported into the logs after 14 years were 0.02 ± 0.03 mg·g⁻¹ in pine logs, 0.03 ± 0.03 mg·g⁻¹ in spruce logs, and 0.07 ± 0.04 mg·g⁻¹ in fir logs. For both N and P, the increases in nutrient content during decay were greatest in logs that had the lowest initial concentration (pine logs for N and fir logs for P).

Litter input

Total annual aboveground litter input averaged 362 g·m⁻² at the pine site, 237 g·m⁻² at the spruce site, and 205 g·m⁻² at the fir site. Foliar litter (needles and leaves) made up the greatest proportion of the litter input at all sites: ca. 40% at the pine site and ca. 50% at the spruce and fir sites (Fig. 4). CWD input accounted for 19% of the litter input at the pine

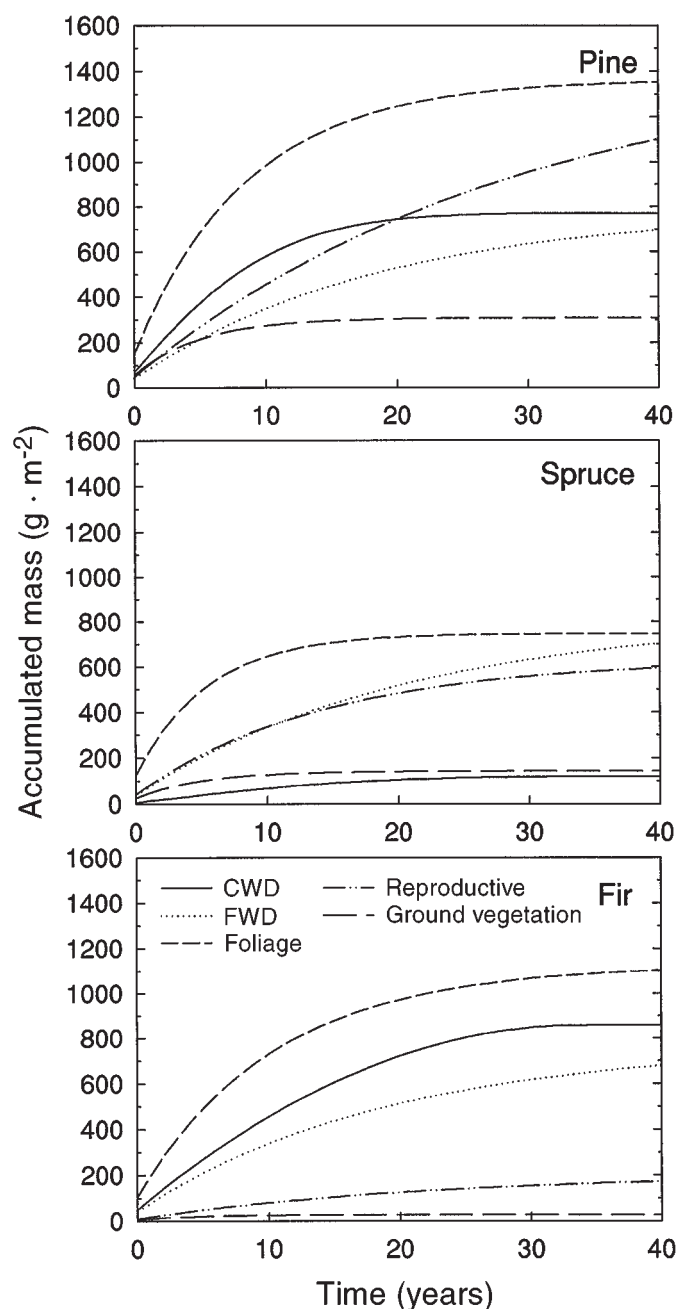
Fig. 4. Average annual inputs of dry mass, C, N, and P in each litter type at the pine, spruce, and fir sites. CWD, coarse woody debris; FWD, fine woody debris. Values are averages of 10 years for CWD, 1 year for ground vegetation, and 5 years for other litter types. Specific materials included in each litter type are described in Methods.



site, 3% at the spruce site, and 24% at the fir site. Expressed as C, these figures were 18, 3, and 23%, respectively.

Total annual N input in aboveground litter was $1863 \text{ mg}\cdot\text{m}^{-2}$ at the pine site, $1484 \text{ mg}\cdot\text{m}^{-2}$ at the spruce site, and $1308 \text{ mg}\cdot\text{m}^{-2}$ at the fir site. The corresponding values for P were 211, 217, and $90 \text{ mg}\cdot\text{m}^{-2}$ per year, respectively. Nonwoody litter, (mostly foliage and cone scales), accounted for more than half of the total aboveground N input

Fig. 5. Contributions of the various litter types to organic matter accumulation at the pine, spruce, and fir sites during a 40-year simulation period. The simulation starts with one annual input. Each year a new cohort is added, and the previous cohorts are decomposed as explained in the Methods.



at all sites (Fig. 4). This was also the case with P input at the spruce and fir sites, but at the pine site, ground vegetation contributed 50% of the annual P input. Ground vegetation also contributed about one third of the annual N input at the pine site and one third of the annual P input at the spruce site. Nutrient input in treefall was very small, accounting for 2.6, 0.4, and 5.1% of the annual aboveground N input and 1.4, 0.5, and 2.2% of the annual aboveground P input at the pine, spruce and fir sites, respectively.

Fig. 6. Contributions of the various litter types to annual C release from the accumulated organic matter (see Fig. 5) at the pine, spruce, and fir sites during a 40-year simulation period.

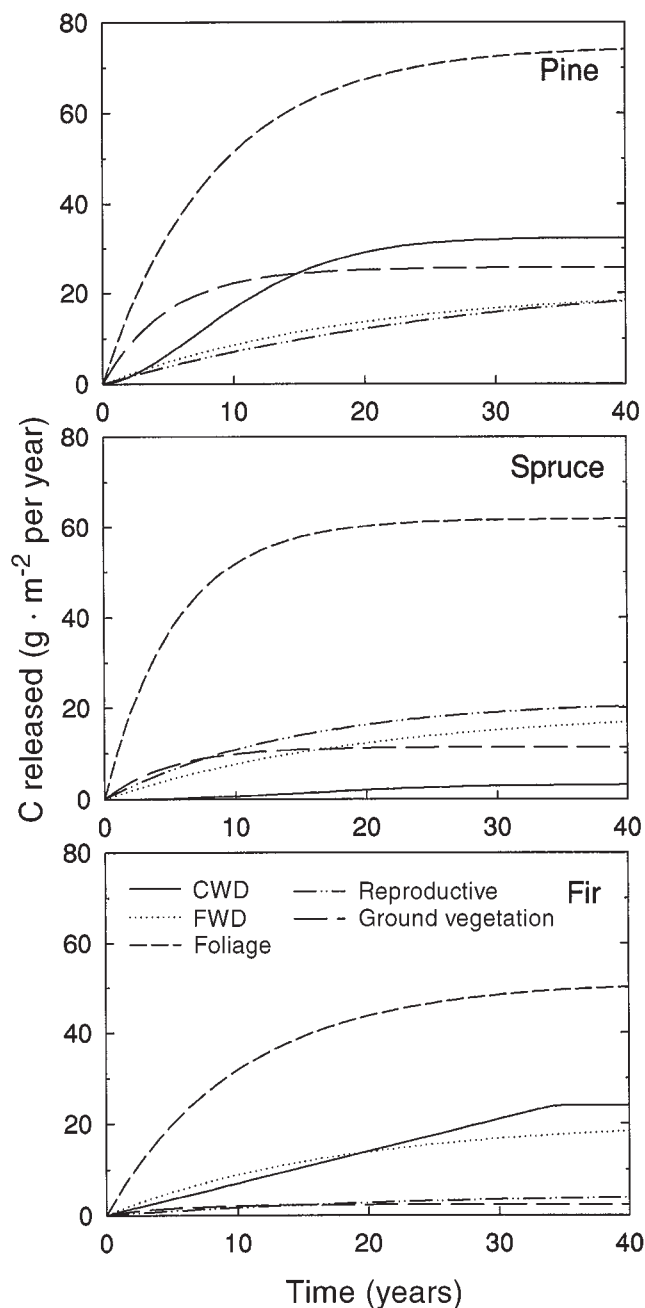
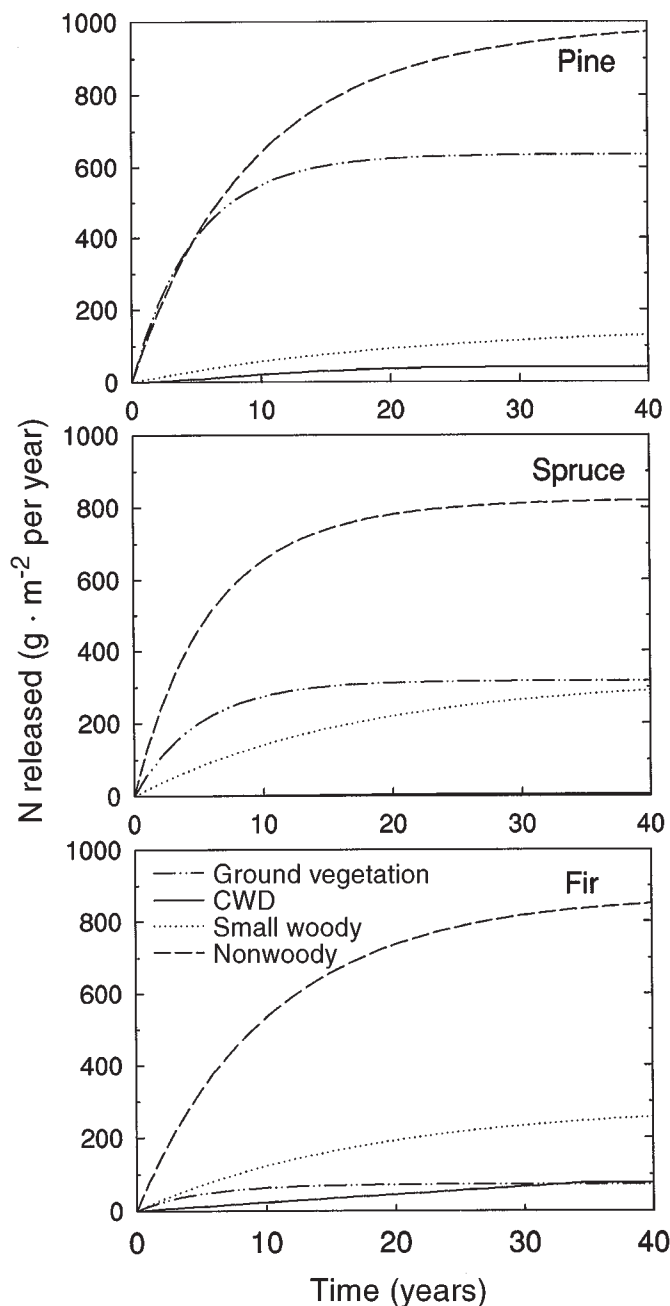


Fig. 7. Contributions of the various litter types to annual N release from the accumulated organic matter (see Fig. 5) at the pine, spruce, and fir sites during a 40-year simulation period.



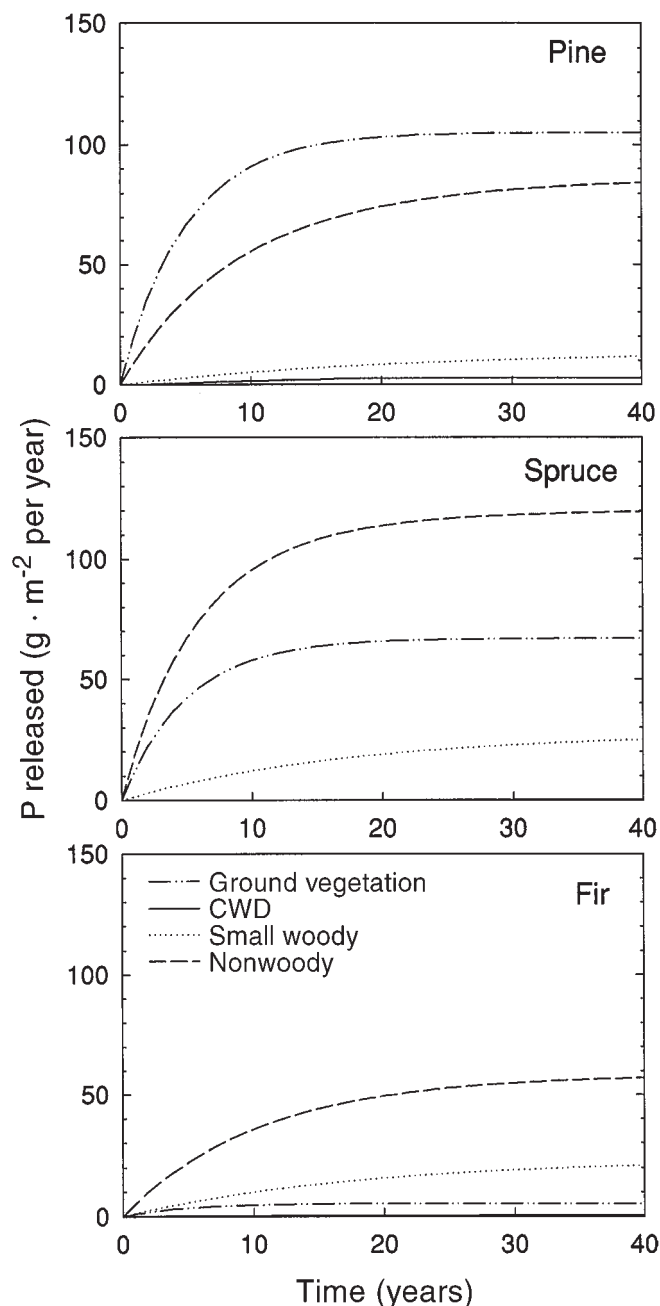
Organic matter accumulation, decomposition, and nutrient release simulations

The accumulation of litter at each site was simulated using the estimates of aboveground litter input presented in Fig. 4 and the decomposition rates of each litter type presented in Tables 1 and 3. The accumulation of most litter components was at or near equilibrium after the 40-year simulation period, i.e., the decomposition rate across all litter cohorts was similar to the rate of input (Fig. 5). The end values of the simulation may thus be used to compare the long-term contributions of different litter components to for-

est floor. The contributions of various litter types to C, N, and P release from the decaying litter materials was estimated by integrating the annual release values over the entire simulation period.

Organic matter accumulation at the end of the simulation period was $4.2 \text{ kg} \cdot \text{m}^{-2}$ at the pine site, $2.3 \text{ kg} \cdot \text{m}^{-2}$ at the spruce site, and $2.8 \text{ kg} \cdot \text{m}^{-2}$ at the fir site. Foliar litter accounted for ca. one third of organic matter accumulated at the pine and spruce sites, and almost 40% at the fir site (Fig. 5). The contribution of CWD to accumulated dry mass was 18% at the pine site, 5% at the spruce site, and 30% at

Fig. 8. Contributions of the various litter types to annual P release from the accumulated organic matter (see Fig. 5) at the pine, spruce, and fir sites during a 40-year simulation period.



the fir site. The corresponding values for the contribution of CWD to accumulated C were 17, 5, and 30%, respectively.

Foliar litter alone accounted for 46% of the C released from decomposing litter at the pine site, 59% at the spruce site, and 56% at the fir site (Fig. 6). CWD accounted for 18% of the total C released from decomposing litter at the pine site, 2% at the spruce site, and 20% at the fir site. Nonwoody litter (mostly foliage and cone scales) also dominated N and P release, especially at the spruce and fir sites (Figs. 7 and 8). Ground vegetation released considerable amounts of both N and P at the pine site. The contribu-

tion of CWD to N and P release was 2% or less except at the fir site where CWD released 5% of the N.

Discussion

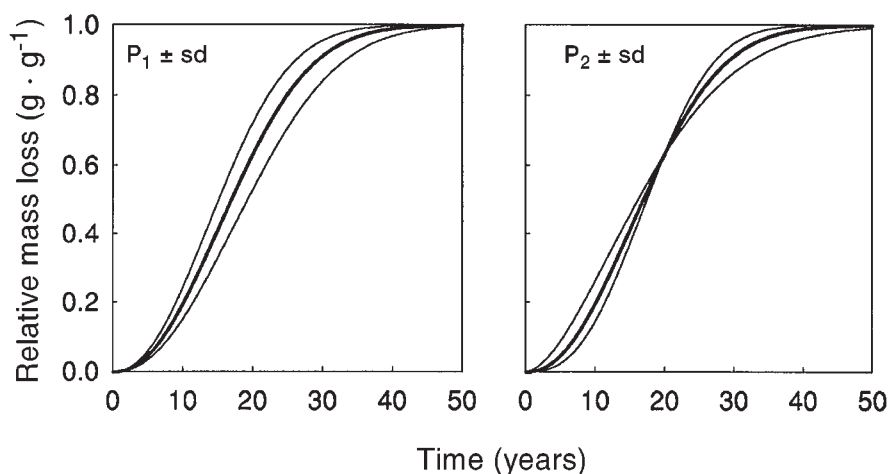
Wood decomposition

Accurate determinations of the pattern of mass loss over time are critical for estimating rates of wood decomposition because using different equation types may lead to very different estimates of turnover time (Graham and Cromack 1982). We found relative dry mass loss from pine logs to follow a sigmoidal relation to time, which contradicts earlier work where exponential (Sollins et al. 1987), linear (Brown et al. 1998), or logarithmic (Grier 1978) relations were suggested. The exponential decay model originally developed for nonwoody litter has often been favoured, as it will provide the decay rate constant k (e.g., Olson 1963). However, an exponential model overestimated decomposition rates of pine logs, and the decay rates of pine and spruce were not constant, as required by the exponential model. A sigmoidal function would account for the slow initial colonization phase, relatively fast decomposition of labile carbon compounds and cellulose and a final slow phase of lignin decomposition (Means et al. 1992). A sigmoidal function might have fitted well to Busse's (1994) density data, where the exponential equation failed to predict the initial lag in decomposition, and residual examination reveals underestimation of decay between ca. 10–20 years and overestimation between ca. 20–40 years. Exponential patterns found by other researchers (Fahey 1983; Sollins et al. 1987) may have resulted from the indirect methods used, particularly the measurement of wood density rather than mass loss. Decay classes are often not well defined (Hope 1987) and indirect methods for estimating log ages may not be reliable (Daniels et al. 1997).

The assumption of sigmoidal mass loss cannot yet be verified for the spruce logs, which had just reached the phase of rapid decay between 10 and 14 years, but the sigmoidal function fit the data with little variation in the parameter estimates (Fig. 9). A sigmoidal function did not fit the mass loss pattern of fir logs, which appeared to be linear after 14 years. The experiment is designed to continue for another 16 years, to assess the validity of the mass loss patterns predicted from the first 14 years.

Although wood decomposition rates may not be constant, estimates of decomposition constants (k -values) may be used to make rough comparisons between different forest types. One must keep in mind methodological differences between studies. Proportional mass loss rates over the entire 14-year study period were 0.0507 for pine, 0.0271 for spruce, and 0.0286 for fir. Our values for spruce and fir logs were close to those presented by Lambert et al. (1980) for balsam fir (*Abies balsamea* (L.) Mill.) in New Hampshire (0.030) and Sollins (1982) and Spies et al. (1988) for Douglas-fir (*Pseudotsuga menziesii* (Mirb.) Franco) in the Pacific Northwest (0.028–0.029). Our value for lodgepole pine logs was much higher than the 0.0163 estimated by Fahey (1983) in Wyoming, and 0.027 by Busse (1994) in central Oregon. Brown et al. (1998) suggested that downed fresh stems of lodgepole pine and Engelmann spruce require over 150 years to completely disappear from high-altitude sites

Fig. 9. Sensitivity of the mass loss equation for spruce logs to variation in parameter estimates. Thick lines are the equation with mean values for the parameters (Table 3); thin lines show variation induced by one standard deviation of the parameter values.



(2990 m) in central Colorado, compared with our estimates of 35–45 years. The lodgepole pine sites studied by Fahey were at higher elevation (2775 m) than our pine site (1530 m), and the pine forest studied by Busse was considerably drier than ours (average annual precipitation 280 mm vs. 660 mm). In our study, mass loss was positively correlated with moisture content in our spruce and fir logs, suggesting that moisture was at least partially limiting log decomposition at the spruce and fir sites but not in the pine site. The moisture content of the logs appears to be influenced by the amount of moss cover on the log; this is likely the effect of the moss layer insulating the log from evaporation losses in summer. The pine logs were highly channelled by carpenter ants by 10 years, which could account for their rapid decay. There was relatively little evidence of insect activity in spruce and fir logs after 14 years. Lodgepole pine has also been found to be less resistant than Engelmann spruce to fungal attack (Eslyn and Highley 1976). Because there was only one species of log at each site, we cannot determine if the faster decay of the pine logs was related to characteristics of the logs or the site.

Assuming that the decomposition continued according to the present estimates, pine logs would disappear completely in about 35 years; spruce logs, in 45 years; and fir logs, in 35 years. These results represent decay rates of logs in direct contact with the ground. The average DBH of the logs used in the decomposition study was 15 cm, which is larger than the mean DBH of downed trees at each site (6.5 cm at the pine site, 13.3 cm at the spruce site, and 9.5 cm at the fir site). Negative relationships have been reported between log diameter and decomposition rate (Stone et al. 1998), so most of the CWD at our sites may decompose faster than our estimates. The effect of log size on decay rate is ambiguous; however, depending on moisture conditions and insect preferences, larger boles may in some cases decompose faster than smaller material (Erickson et al. 1985; Edmonds and Eglitis 1989), and in some cases no size-related differences have been found (Busse 1994).

The end pieces lost mass faster than the center pieces, indicating that microbial colonization of the ends was more rapid than the centers. Thus the 3-cm end pieces appeared to

reduce the artificial hastening of decomposition resulting from exposure of cut ends. The differences were consistently significant only in the fir logs, which probably reflects different decay mechanisms of fir compared with pine and spruce. Fir logs retained their bark which provides some protection against fungal colonization (Hintikka 1973), whereas pine and spruce logs lost most of their bark. Thus, the exposed log ends would be a more important pathway for colonization in the fir logs. In pine logs, decomposition was most advanced on the bottom of the logs, so the cut ends appeared to be less important.

Nitrogen and phosphorus release from decaying wood

Most studies of nutrient release from decaying wood have shown increases in N contents until decomposition is well advanced, and a steady decline in the K content. Release patterns of other elements have been highly variable (Lambert et al. 1980; Graham and Cromack 1982; Fahey 1983; Sollins et al. 1987; Arthur and Fahey 1990; Hart 1999). In this study, nutrient release during the first 14 years of log decomposition differed between the two elements (N and P) and also among the three species of logs. The pine logs gained N, spruce logs released some N, and the fir logs released almost 30% of their original N content. This pattern was related to the initial N concentrations in the logs, which were lowest in the pine logs and highest in the fir logs. A similar pattern was even more striking for P: the fir logs with very low initial P concentration immobilized additional P equivalent to almost four times their initial content. The net import of P during the 14 years was greatest in the fir logs and least in the pine logs, which had the highest initial P concentration. Wells and Boddy (1990) and Wells et al. (1990) have shown that wood-decaying fungi translocate P from surroundings to the substrate they are colonizing. Apparently, the poorer the initial substrate in N or P, the more translocation takes place. Nitrogen and P release dynamics of other litter types have been found to depend on the initial concentrations (Prescott et al. 1993), and a similar pattern was noted for decaying wood (Alban and Pastor 1993). Earlier studies at these sites indicated that N was the most limiting nutrient for vegetation at the pine site, and P was most

limiting at the fir site (Prescott et al. 1992). Our findings of greatest N import into logs at the pine site and greatest P import at the fir site suggest that wood decay organisms may be competing with vegetation for limiting nutrients. Some of the N imported may be from N fixation in the logs, which has been reported in Rocky Mountain forests (Jurgensen et al. 1987). Applying the estimated annual rate of N fixation of 0.01 mg N-g^{-1} presented by Jurgensen et al. (1987), N fixation could account for about half of the net N import in pine logs over the 14 years.

Role of CWD in C, N, and P release

Based on our simulation of input and decomposition of aboveground litter, CWD played a rather insignificant role in the N and P release in these forests (Figs. 7 and 8). The contribution of CWD to N and P release was 2% or less except at the fir site where CWD released 5% of the N. These estimates are only valid for these forests at the time of measurements, but the sites represent a variety of common forest types and stand development stages: a dense self-thinning lodgepole pine stand, a mature post-thinning spruce stand, and an old-growth spruce–fir stand.

Our simulation represents a hypothetical situation where litter input rates would remain constant for 40 years. The variation in the annual inputs within our 5-year (nonwoody and small woody litter) or 10-year (CWD) measurement periods did not show any significant trends. Johnson and Fryer (1989) have studied tree population dynamics in fire-originated lodgepole pine – Engelmann spruce forests in the Kananaskis Valley. They found that lodgepole pine mortality increased when the stands entered the self-thinning phase at about 25 years and reached its maximum at around 90–100 years, after which it remains more or less constant until at least 200 years. The mortality rate of Engelmann spruce was relatively constant irrespective of stand age. This would indicate that no great changes in rates of CWD input are expected in our pine and spruce stands within the next 40 years. Sollins (1982) found no obvious pattern of CWD input with time or with stand age in coniferous stands in western Oregon and Washington, although many of the highest values were from an old-growth site. Sollins (1982) also suggested that values based on intervals <10 years would be potentially misleading because of the high temporal variation. Albrektson (1988) found no clear relation between input of foliar litter and stand age in Scots pine (*Pinus sylvestris* L.) stands, although it would be expected to increase until the stand achieves maximum foliar biomass. The greatest uncertainty in the simulation is arguably the decay rates of small woody litter, which had not advanced very far during the 4-year litter decomposition experiment described by Taylor et al. (1991). Overall, our simulation should provide a reasonable indication of the relative importance of the different litter components in C, N, and P release in these forests. The simulated relative contributions of CWD to the accumulated organic matter (Fig. 5) agreed well with the measured amounts of surface wood relative to total forest floor masses at the pine (18 vs. 20%) and spruce (5 vs. 8%) sites (Prescott et al. 1989b, data for Fig. 3), although the simulation overestimated (30 vs. 15%) the contribution of CWD at the fir site.

Another potential weakness of our simulation was that, although we used input data for each tree species, the decomposition rates of CWD at each site were based on measurements of the one dominant species only. However, at the pine site, only 8% of the mass of CWD input was from species other than pine; at the fir site, 13% was from species other than fir. At the spruce site, 26% of the mass of CWD input was from species other than spruce (mostly balsam poplar). This decay rate of poplar may be different from spruce; however, given the low rates of CWD input at this site, it is unlikely that this would alter our conclusion regarding the importance of CWD in nutrient cycling.

Other studies have also indicated that the contribution of CWD to nutrient cycling in undisturbed forests is relatively minor. According to Busse (1994), downed wood comprised less than 3% of the soil nutrient pools in lodgepole pine stands in central Oregon. Fahey et al. (1985) found that downed wood accounted for less than 3% of the soil N pool in two lodgepole pine ecosystems in Wyoming. The interpretation of these pool values is not unambiguous, however, because the CWD pool may include N imported from the surroundings, and the soil organic matter pool contains an unknown proportion of N derived from CWD. Estimates of nutrient release from CWD are still scarce. In a old-growth forest of Douglas-fir, western hemlock (*Tsuga heterophylla* (Raf.) Sarg.), and western red cedar (*Thuja plicata* Donn.) in central Oregon, Hart (1999) estimated that well-decayed logs contribute only 4–6% of annual plant N uptake.

CWD clearly has more importance for the C flows. CWD accounted for 18% of the C in aboveground litter input at the pine site, 3% at the spruce site, and 23% at the fir site. CWD contributed 17% of the C accumulating from aboveground litter at the pine site, and 30% at the fir site. The simulated contribution of CWD at the spruce site, 5%, was lower, reflecting the very low rates of treefall in this mature, low-density stand. Busse (1994) estimated that downed bole wood accounted for 68% of the total detrital (forest floor + wood) C pool in lodgepole pine forests in central Oregon. The proportion of CWD in organic matter accumulation may vary considerably among different forest types (e.g., Jurgensen et al. 1997) as well as within one type: in lodgepole pine forests studied by Fahey (1983) the variation ranged from 6% in an old-growth stand to 45% in a dense 105-year-old stand.

According to our simulation, CWD contributed 18% of the C released from decaying aboveground litter at the pine site, 2% at the spruce site, and 20% at the fir site. Ground vegetation had a prominent role in N and P cycling at the pine and spruce sites, especially in light of the relatively small mass of this material. The amount of P released from ground vegetation litter at the pine site was similar to P release from overstorey litter. Ground vegetation litter had relatively high N and P concentrations (Table 2) and it decayed relatively fast (Table 1). Thus, ground vegetation may play a key role in maintaining N and P availability in these forests.

In conclusion, our findings indicate that CWD is not a significant source of available N and P in these forests; it may actually compete with vegetation for limiting nutrients. Given the small nutrient concentrations in CWD, large amounts of CWD would have to be left on site after harvesting to obtain any significant N and P storage. Guidelines for

management of CWD should be based on its other potential values, which will vary among ecosystems. CWD may be important in base cation cycling in base-poor ecosystems (Arthur and Fahey 1990). Where other litter components decay rapidly, or where frequent fires occur, CWD may have an important role in maintaining a surface organic layer. In dry forests, CWD may retain moisture and may be a source of water for vegetation during droughts. In coastal forests of the Pacific Northwest decaying boles act as a critical site for seedling establishment (Harmon et al. 1986). Decaying wood serves as a critical habitat for many types of organisms (Freedman et al. 1996). The amounts of woody debris to be maintained should be based on management objectives related to these values, rather than its role in N and P cycling. For sustaining site productivity, the essential question is whether the total nutrient pool left on site (rather than the amount of CWD), and the rate of nutrient input through weathering and precipitation, are large enough to offset the loss of nutrients in harvested timber. For maintaining nutrient availability, management of faster recycling materials such as ground vegetation and nonwoody litter may be more critical than maintaining CWD.

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